The Systematics of the Prickly Sculpin, *Cottus asper* Richardson, a Polytypic Species
Part I. Synonymy, Nomenclatural History, and Distribution[1]

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ABSTRACT: The prickly sculpin, *Cottus asper,* is a geographically widespread, polytypic species characteristically represented by very prickly, nonmigratory, fresh-water spawning "inland" forms, and less prickly, catadromous, brackish-water spawning "coastal" forms. Part I, the first contribution in a series on the systematics of this species, presents a synonymy complete for the period 1836–1936, with a resumé of the most important citations from 1936 to 1965. A nomenclatural history of the species is given. The distributional range is listed and also presented in illustration.

The prickly sculpin ranges over about 3,000 miles of Pacific North Temperate coastline and inland as far as 300 miles. The species exists in two primary modes of morphological variability: one, a nonmigratory, fresh-water spawner, has extensive squamation on certain regions of the body; the other, a catadromous, brackish-water spawner, has little or none. Prickly sculpin eggs are spawned naturally in environments which are known to vary in at least one major factor, i.e., salinity. The morphological, behavioral, and ecological variations existing within this species make it an excellent subject for systematic analysis.

SYNONYMY

It has been 130 years since *Cottus asper* was first described by Sir John Richardson. Prior to the present study, regional systematic treatments of this widespread species resulted in a proliferation of generic and specific taxa, all referable to *C. asper.* Early revisionary work by Girard in 1851 and 1852 was incomplete because of lack of specimens. Recent regional works (Robins and Miller, 1957; McAllister, 1957; McAllister and Lindsey, 1959; and Bond, 1963) have included the species as part of a geographical area or river drainage system, but there has never been a comprehensive treatment of the species throughout its entire range. In the period 1836–1936, 41 reports of *C. asper* were cited in the literature. In the same period, 32 additional citations occurred which were either misidentifications or synonyms properly referable to *C. asper.* In none of the systematic treatments published since the original description in 1836 has there been a synonymy containing more than 7 citations. McAllister (1957) listed 15 citations in his unpublished M.A. thesis.

The present synonymy consists of 73 citations published during the period 1836–1936, and is thought to be complete for that period. In the past 30 years, the species has been cited incidentally in so many fishery journals and publications that only the major systematic, or otherwise noteworthy, citations have been reported in the remaining synonymy.

Cottus asper Richardson, 1836

Cottus asper. Richardson, 1836:295, pl. 95, fig. 1 (original description and figure; Columbia R.; collected by Dr. Gairdner, probably near Fort Vancouver, Washington Territory). Storer, 1846*a*:260, and 1846*b*:8 (northwestern coast of N. America). Girard, 1850:409, and 1851*a*:189 (discusses propriety of present

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nomenclature). Eigenmann, 1895:118 (abundant in Fraser system from tidewater to 1,900 ft; Mission, Sicamous, Kamloops, and Griffin L., British Columbia; and Umatilla, Oregon). Gilbert and Evermann, 1895:201 (description; comparison with Sacramento R. form; Walla Walla R. at Wallula, and Lake Washington, Washington). Seale, 1896:854 (Lake Washington). Gilbert, 1896:418 (description; stream entering Departure Bay, Vancouver Island). Jordan and Evermann, 1896: 439 (synonymy; streams of the Cascade Range, from Vancouver Island to Oregon). Gilbert, 1898:1 (Columbia R.; notes absence in Klamath R.). Jordan and Evermann, 1898:1944 (description; synonymy; Walla Walla; Departure Bay; about Port Townsend; streams of the Cascade Range, from Vancouver Island to Oregon). Evermann and Meek, 1898:83 (Lake Washington). Meek, 1899:231 (Lake Southerland, Olympic Peninsula, Washington). Jordan, 1905:445 (streams of the Pacific coast). Snyder, 1905:337 (description; affinities; habitat preference; San Franciscito, Madera, San Antonio, Guadalupe, Coyote, and Alameda creeks, all flowing into San Francisco Bay). Evermann and Goldsborough, 1907*a*:306 (characters; prickling descriptions; Deep Bay, Naha R., and Steelhead Cr., Loring, Alaska; Hunter Bay, Yes Bay, and McDonald L., Alaska). Evermann and Goldsborough, 1907*b*: 110 (Fraser R. at Mission, Shuswap L. at Sicamous, Thompson R. at Kamloops, and Griffin L.). Rutter, 1908:145 (*Cottopsis parvus* first placed in synonymy with *asper;* synonymy, in part, except *Uranidea semiscaber* (sic) *centropleura* Eigenmann and Eigenmann; summary of 9 localities in Sacramento R. system). Snyder, 1908*a*:269 (Russian R., California). Snyder, 1908*b*:184 (characters; prickling description; summary of 41 localities: from Lake Washington, Columbia and Sacramento R., and river basins in between). Nichols, 1909:172 (head of Chilkoot L., Alaska). Evermann and Latimer, 1910:138 (4 localities in Marin Co., and 2 localities in San Francisco Bay, California; 12 localities in Olympic Peninsula, Washington). Snyder, 1913:72 (characters; Pajaro R., California). Snyder, 1916:381 (Papermill and Walker creeks, California). Kermode, 1917:20 (Hanceville, British Columbia [Chilcotin R. drainage]). Jordan, 1919:249 (designates *Cottus asper* Richardson as the orthotype of *Cottopsis* Girard). Bean and Weed, 1920:76 (mouth of Fraser R.). Hubbs, 1921:7 (reidentification of San Luis Cr., California, specimens misidentified by Jordan as *C. gulosus* [1895:141]; range extension to Ventura R., California). Fowler, 1923:282 (Hanceville, and Shawnigan L., British Columbia; Shawnigan L. specimen misidentified by Kermode [1909:87] as *Uranidea gulosa*). Crawford, 1927:177 (streams flowing into Puget Sound). Schultz, 1929:48 (listing only). Schultz, 1930: 14 (most streams and lakes of western Washington). Jordan, Evermann, and Clark, 1930: 383 (synonymy; streams of the Cascade Range, southeastern Alaska to Oregon; south to Sacramento R.). Kermode, 1931:19 (Cowichan L., Vancouver Island). Evermann and Clark, 1931: 56 (summary of 32 recorded localities in California). Taft, 1934:251 (spawning migration). Schultz and DeLacy, 1936*a*:128 (synonymy; coastal streams from Alaska to Ventura Co., California; fresh water and brackish water; review of most records from Puget Sound to Oregon, and addition of 26 more localities). Schultz and DeLacy, 1936*b*:213 (additional synonymy; 3 new localities). Schultz, 1936:179 (keys to species of *Cottus;* coastal streams from Alaska to Ventura Co., California; fresh-water and brackish). Dymond, 1936:71 (description; throughout southwestern British Columbia, including southern Vancouver Island; 16 localities listed). Sumner, 1942:1–25 (common in tidewater areas along the Oregon coast). Hubbs and Wallis, 1948:141 (identification of "*Cottus* sp." recorded by Dill, 1946:54). Bailey and Dimick, 1949:14 (comparison with *Cottus hubbsi*). Shapovalov and Dill, 1950:387 (listing only). Wilimovsky, 1954:285 (southeast Alaska to California). Robeck, et al., 1954: B–65 (Columbia R., above Trinidad, Washington; cited as "prickly sculpins *Cottus* sp.," these may include *Cottus rhotheus* in part). Lindsey, 1956:777 (Pacific Slope of N. America from Alaska to California; British Columbia mainland from Columbia, Fraser, and Skeena systems, Stikine R. headwaters, and Peace R. [Summit L., Heart L., Angusmac Cr., and McLeod L.]). Robins and Miller, 1957:229 (*Cottopsis parvus* again removed from syn-

onymy of *C. gulosus*). Lindsey, 1957:657 (British Columbia: Columbia R.; Fraser R.; Skeena R.; coast drainages south of Skeena; Nass R.; Stikine R.; Peace R.). Wilimovsky, 1958:62 (key to species in Alaska; southeast Alaska to California). Shapovalov, Dill, and Cordone, 1959:173 (listing only). Carl, Clemens, and Lindsey, 1959:158 (description; Pacific drainages from Chilkoot L., Alaska, to Ventura R., California. In British Columbia: lakes and rivers of the Columbia, Fraser, Dean, Skeena, Nass, and Stikine systems; coastal rivers of the mainland and Vancouver Island, and Queen Charlotte Islands; headwaters of Peace R. system from Summit L. to McLeod L.). McAllister and Lindsey, 1959:70 (description; synonymy; intraspecific variation; localities as in Carl, Clemens, and Lindsey, 1959). McAllister, 1960:42 (collection in salt water, Pt. Atkinson, British Columbia). Bond, 1961:36 (key to species in Oregon; prickling variation; Columbia R. drainage). Bond, 1963: 79 (synonymy; life history observations; oxygen, temperature, and salinity tolerance of adults; fish associates; habitat preference; lists 35 new collection localities in coastal Oregon, 30 localities from Columbia R. drainage in Oregon, and also some lakes in the southwest corner of Rainier National Park, Washington). Bailey and Bond, 1963:19 (recognition of several species groups within *Cottus* in western N. America; characters and list of species in the "*asper* species group"). Krejsa, 1965:1–109 (synonymy; nomenclatural history; distribution; life history; morphological variation; salinity tolerance of eggs; phylogeny of *C. asper* and closely related species). Bohn and Hoar, 1965: 977 (salinity effects on iodine metabolism; physiological divergence of inland and coastal *C. asper*).

Centridermichthys asper. Richardson, 1844:76 (River Oregon [= Columbia R.]). Günther, 1860:170 (description; synonymy; fresh waters of the Oregon and Washington Territories). Lord 1866*a*:130 (life history; spawning behavior, in part; Puget Sound; "streams flowing through the Sumass and Chilukweyuk prairies" [Sumas and Chilliwack R. ?], British Columbia; in part, all streams east and west of the Cascades).

Cottopsis asper. Girard, 1851*b*:303 (introduction of *Cottopsis* gen. nov.; synonymy; limited to River Oregon [= Columbia R.]). Girard, 1851*c*:185 (not seen). Girard, 1852:61 (definition of *Cottopsis* gen. nov., based on Richardson's description of *Cottus asper;* synonymy; Columbia R.). Girard, 1859:51 (description; synonymy; based on 8 specimens from Astoria and Fort Dalles, Oregon, and Fort Steilacoom, Puget Sound, Washington Territory). Suckley (in Cooper and Suckley, 1859) 1859:351, and Suckley, 1860:351 (description; synonymy; small fresh-water streams emptying into Puget Sound; Ft. Steilacoom; and Columbia R., 200 miles above mouth). Jordan and Jouy, 1882:5 (Puget Sound; Columbia R.; Mare Island and Sacramento R., California).

Uranidea aspera. Jordan and Gilbert, 1883:694 (description; synonymy; streams west of the Sierra Nevada and Cascade Mountains). Jordan, 1885: 110 (subgenus *Cottopsis* and a list of species therein).

Trachidermus richardsonii. Heckel, 1840:162 (synonymy; Columbia R.), (not *Cottus richardsoni* of Agassiz, 1850). Note: Girard, 1852:62, erred in reporting the date of Heckel's paper as 1837, and in the spelling of *Trachidermus.*

Cottopsis parvus. Girard, 1856*b*:144 (original description; Presidio on San Francisco Bay, California). Girard, 1857:11 (description; Presidio, and Monterery, California). Girard, 1859:54 (description; synonymy; Monterey, Presidio, Fort Reading, and Petaluma, California). Cooper, 1868:492 (listing only). Jordan, 1877:5 (as the young of *Cottopsis asper*).

Centridermichthys parvus. Günther, 1860: 170 (description; synonymy; fresh waters of California). Lord, 1866*b*:352 (listing; "frequenting the same localities as . . ." *Centridermichthys asper*).

Uranidea aspera var. *parvus.* Jordan and Gilbert, 1883:694 (Sacramento R. forms).

Cottus gulosus parvus. Jordan and Evermann, 1898:1945, and Jordan, Evermann, and Clark, 1930:383 (*Cottopsis parvus*: Monterey, Presidio, Fort Reading, and Petaluma, California).

Uranidea gulosa, in part. Jordan and Gilbert, 1883:695 (misidentifications: all specimens from "Vancouver's Island" and probably those from "about Port Townsend," cf. Jordan and Evermann, 1898:1944). Kermode, 1909:87 (listing only; misidentification: Shawnigan L., Vancouver Island, cf. Fowler, 1923:282).

Cottus gulosus, in part. Jordan, 1895:141 (misidentification: San Luis Cr., near Avila, California, cf. Hubbs, 1921:7). Jordan and Evermann, 1898:1945 (misidentification: all specimens from San Franciscito Cr., Santa Clara Co., California). Jordan, Evermann, and Clark, 1930:383 (probable misidentifications: specimens from Loring and Boca de Quadra, Alaska). Evermann and Clark, 1931:57 (misidentifications: Presidio, Monterey, Fort Reading, Petaluma, and San Luis Cr., California). Evermann and Clark, 1931:12, 13 (misidentifications: Monterey, Presidio, Fort Reading, and Petaluma). Bean and Weed, 1920:76 (questionable identification: 4 specimens from Victoria, Vancouver Island, British Columbia). Wilimovsky, 1954:285 (doubts validity of southeast Alaska record).

Centridermichthys gulosus. Lord, 1866*b*: 352 (listing; "frequenting the same localities as . . ." *Centridermichthys asper*).

Cottus sp. Dill, 1946:54 (San Joaquin R., near Friant, California; identification as *asper* by Hubbs and Wallis, 1948:141).

NOMENCLATURAL HISTORY

The specific name *asper* is currently well founded in the genus *Cottus,* to which it was originally designated by Richardson in 1836. But, as shown in the preceding synonymy, the binomen was extremely unstable for the first 100 years after its introduction. After an initial period of uncertainty regarding its affinity to marine or to fresh-water Cottoids, three main nomenclatural difficulties are encountered: the often-repeated misidentification as *Cottus gulosus* (Girard); the failure to recognize that *Cottopsis parvus* and *Cottus asper* are conspecific; and the failure to recognize the specific relationship of *asper* to other species in the genus *Cottus.*

The almost immediate placement of *asper* into *Trachidermus* by Heckel (1840), and then into the synonymous *Centridermichthys* by Richardson (1844), reflects the early opinion that *asper* was more closely allied to the marine Cottoids. Girard (1851*b,* 1852) recognized its affinities with the fresh-water genus *Cottus,* but distinguished it from that genus by erecting the genus *Cottopsis,* based on the presence of palatine teeth and the "skin beset with prickles, instead of being smooth and scaleless." Lacking any specimens, Girard defined *Cottopsis* on the basis of Richardson's original description but, on p. 63, where he quoted Richardson's entire discussion of prickles (p. 295), he misquoted Richardson by attributing to him the statement, "There are no scales." Girard's lack of specimens proved unfortunate since soon thereafter (1856*b*) he named and described *Cottopsis parvus* from the Presidio (in San Francisco), California, comparing it not with *C. asper* but with *Cottopsis gulosus* Girard, also newly described (1856*a*) from the San Joaquin R., California. In his later report (1859), Girard had 8 specimens of *C. asper* in his possession, from the Columbia R. and Puget Sound. Obviously he again failed to recognize the conspecificity of *asper* and *parvus,* and he followed Richardson's original description rather than comparing them with specimens of *parvus,* which he seems to have reserved for comparison with *gulosus.*

Jordan (1877) referred, in passing, to *Cottopsis parvus* as the young of *C. asper.* Jordan and Jouy (1882), however, listed specimens of *Cottopsis asper* from Mare Island and Sacramento R., California, *and* from Puget Sound and the Columbia R. Less than a year later, Jordan and Gilbert (1883) placed *asper* in the genus *Uranidea* DeKay, subgenus *Cottopsis,* based on the presence of palatine teeth and the gill membranes being broadly united to the isthmus. In the same report, they referred to the Sacramento R. form of *U. aspera* as "var. *parvus,* smaller in size, paler in color and with the interorbital space concave, narrower than eye."

Eigenmann (1895) used the valid name to describe specimens from the Fraser and Columbia rivers, as also did Gilbert and Evermann (1895), who suggested that the nominal spe-

cies was separable "at least subspecifically from the Sacramento River form." Seale (1896) and Gilbert (1896) used the valid name for northern specimens. But, obviously, Jordan (1895) and Jordan and Evermann (1896) still thought in terms of a distinct Californian species (*gulosus*) and a distinct northern species (*asper*). Jordan misidentified a specimen of *asper* from San Luis Cr., near Avila, Calfornia, as *gulosus*. Jordan and Evermann listed the range of the nominal species from Vancouver Island to Oregon, and of *gulosus,* from California Coast Range streams and inland in the San Joaquin R. Gilbert (1896) referred to *Cottus asper* of the Columbia and *Cottus gulosus* of the Sacramento as "two species so extremely similar that it is difficult to distinguish them." Jordan and Evermann (1898) repeated the suggestion of Gilbert and Evermann that the nominal species is separable, at least subspecifically, from the Sacramento R. form, "*Cottus gulosus.*"

That Jordan and Evermann perceived neither the conspecific relationship of *parvus* to *asper* nor the limits of the valid species *Cottus gulosus* becomes more fully evident on the next page (p. 1945) of their 1898 report. Their description of *Cottus gulosus* (Girard) is taken from misidentified specimens of *C. asper* collected in San Franciscito Cr., Santa Clara Co., California. These were large specimens "3 to 7 inches in length" and, most significantly, the count for anal rays is given as "A. 16 to 18." Both of these characters separate *asper* from *gulosus*. Furthermore, they include *Cottopsis parvus* Girard, from Monterey, the Presidio, Fort Reading, and Petaluma, California, in the synonymy of *gulosus.*

Snyder (1905) collected and correctly identified *Cottus asper* from the same locality, San Franciscito Cr. He was probably the only one of his time to understand and explain the true relationships of *asper, parvus,* and *gulosus*. On p. 337, he stated:

> Recent authors have identified the common Sacramento form which represents the *Cottus asper* of the Columbia River with the *Cottopsis gulosus* of Girard. They have sometimes considered the Sacramento form as identical with *C. asper* and have placed the name *gulosus* in the synonymy of the latter. At other times they have considered the species as a slightly differentiated form worthy of recognition in nomenclature, and have used the name *gulosus* to designate it. The former view concerning the species is probably correct. The association of the name *gulosus* with it, however, is without warrant. The latter belongs to a species easily distinguished from *C. asper,* differing notably in having a much shorter anal fin. There are usually fewer dorsal spines and rays, a more limited distribution of prickles, and an almost uniform absence of palatine teeth. In *C. asper* the dorsal has 8 to 10 spines and 19 to 22 articulated rays, the anal 16 to 18 rays, while in *C. gulosus* the dorsal has 7 to 9 spines, 17 to 18 rays, the anal 12 to 14 rays.

Snyder then continues with a note on habitat preference:

> In its distribution *C. asper* appears to be largely confined to the lower courses of the streams, being especially abundant near tide water, while *C. gulosus* is found further up, where the water is clear and the current rapid.

Rutter (1908) correctly placed *Cottopsis parvus* into the synonymy of *Cottus asper,* presumably recognizing that the two were conspecific. However, he incorrectly synonymized *Uranidea semiscabra centropleura* Eigenmann and Eigenmann, which is properly referable to *Cottus gulosus.*

Snyder was the first to consider a series of specimens of the nominal species throughout its entire range, as then known, and, in the same issue of the Bulletin of the Bureau of Fisheries in which Rutter had correctly synonymized *parvus,* he noted the extreme variation of prickling investment. While recognizing the variation between streams, he also noted that the prickling variation is common among individuals from the same stream.

Although explicitly aware of Snyder's comments on *asper* and *gulosus,* Evermann and Goldsborough (1907*a*) identified 16 specimens of *gulosus* from Loring and Boca de Quadra, Alaska. The reliability of these identifications is questionable. Kermode's listing (1909) of *Uranidea gulosa* from Shawnigan L., Vancouver Island is probably a misidentification, since Fowler (1923:282) listed the same specimen as *Cottus asper.*

Snyder (1913, 1916) again recorded the occurrence of *C. asper* and *gulosus* in differing habitats of the same stream. Hubbs (1921) recognized Jordan's earlier misidentification of *gulosus* from San Luis Cr., California. He also commented on the variability of prickling in *C. asper* from several streams.

It would seem that with the accession of Snyder's insight into the problem, the valid name was destined for stability. However, Jordan, Evermann, and Clark (1930) repeated the earlier error of Jordan and Evermann (1898) by including *Cottopsis parvus* as a synonym of *Cottus gulosus.* In a similar manner, they also incorporated the error of Evermann and Goldsborough (1907*a*), previously cited, by including the misidentified specimens of *asper* from Loring and Boca de Quadra, Alaska, in the list of records for *gulosus.* In the same work, Jordan and Evermann extended the range of *asper* (cited in 1898 as: "streams of the Cascade Range, from Vancouver Island to Oregon") by appending the phrase "south to Sacramento River." Evermann and Clark (1931) also retained *Cottopsis parvus* in the synonymy of *C. gulosus* and perpetuated Jordan's misidentification of the San Luis Cr. *gulosus,* which Hubbs had correctly re-identified as *asper* ten years before (1921).

Schultz and DeLacy's catalogue (1936) included a comprehensive listing of Washington and Oregon localities for *C. asper.* However, some remain doubtful since Schultz and DeLacy frequently misidentified *C. asper* as *gulosus* and/or *perplexus.* They also incorrectly maintained the presence of *C. gulosus* in Alaska.

Robins and Miller (1957) presumably overlooked the earlier citation of Rutter (1908) and removed *Cottopsis parvus* from the synonymy of *gulosus,* placing it in the synonymy of *asper,* supposedly for the first time.

McAllister and Lindsey (1959) first suggested the probable existence of "coastal" and "non-coastal" populations of *Cottus asper* on the basis of morphological and, perhaps, behavioral differences.

Bond (1961) hinted at the possibility of polytypy in *Cottus asper* when he stated in his key that the body is "well covered with prickles, especially in inland waters and in young individuals from coastal waters." Bond (1963) gave the most comprehensive treatment yet recorded for *Cottus asper* and 12 other species in the genus. His study, however, was more concerned with interspecific rather than intraspecific relationships within the genus. Bailey and Bond (1963) indicated their concern for the supraspecific relationships within the genus *Cottus* by their recognition of several species groups, one of which is the "*asper* species group."

Krejsa (1965) offered morphological, behavioral, and distributional evidence for genetic divergence between "coastal" and "inland" populations of *C. asper.* Bohn and Hoar (1965) offered physiological evidence in support of Krejsa's hypothesis. Unfortunately, their brief introductory remarks regarding the life histories and prickling patterns are somewhat inaccurate, and therefore misleading, interpretations of Krejsa's unpublished thesis. These minor points will be clarified in a future publication.

DISTRIBUTION

Range. Pacific Slope drainage of North America: coastal streams from Seward, Alaska, to Ventura R., California; lakes and streams of the Queen Charlotte Islands and Vancouver Island; and all major Pacific drainages from the headwaters of the Stikine R. in British Columbia, to the Kern R., San Joaquin R. drainage, California. The following are exceptions: Fraser R. in the area of the Rocky Mountain Trench, east of Prince George, British Columbia (area not yet collected); Kootenay Lake drainage of the Columbia R. in British Columbia; Upper Snake R. of the Columbia R. drainage in Washington and Oregon; Middle Fork of the Willamette R. in Oregon, above Oakridge; Klamath R. Basin in Oregon; and Sacramento R. drainages above Lake Shasta, California. Arctic Slope drainage of North America: headwaters of the Peace R. in British Columbia: from Summit L. to McLeod L., Crooked R. drainage; from Tacheeda L., Parsnip R. drainage; from Tchentlo L., Nation R. drainage.

The present distributional range of *Cottus asper* is illustrated in Figure 1.

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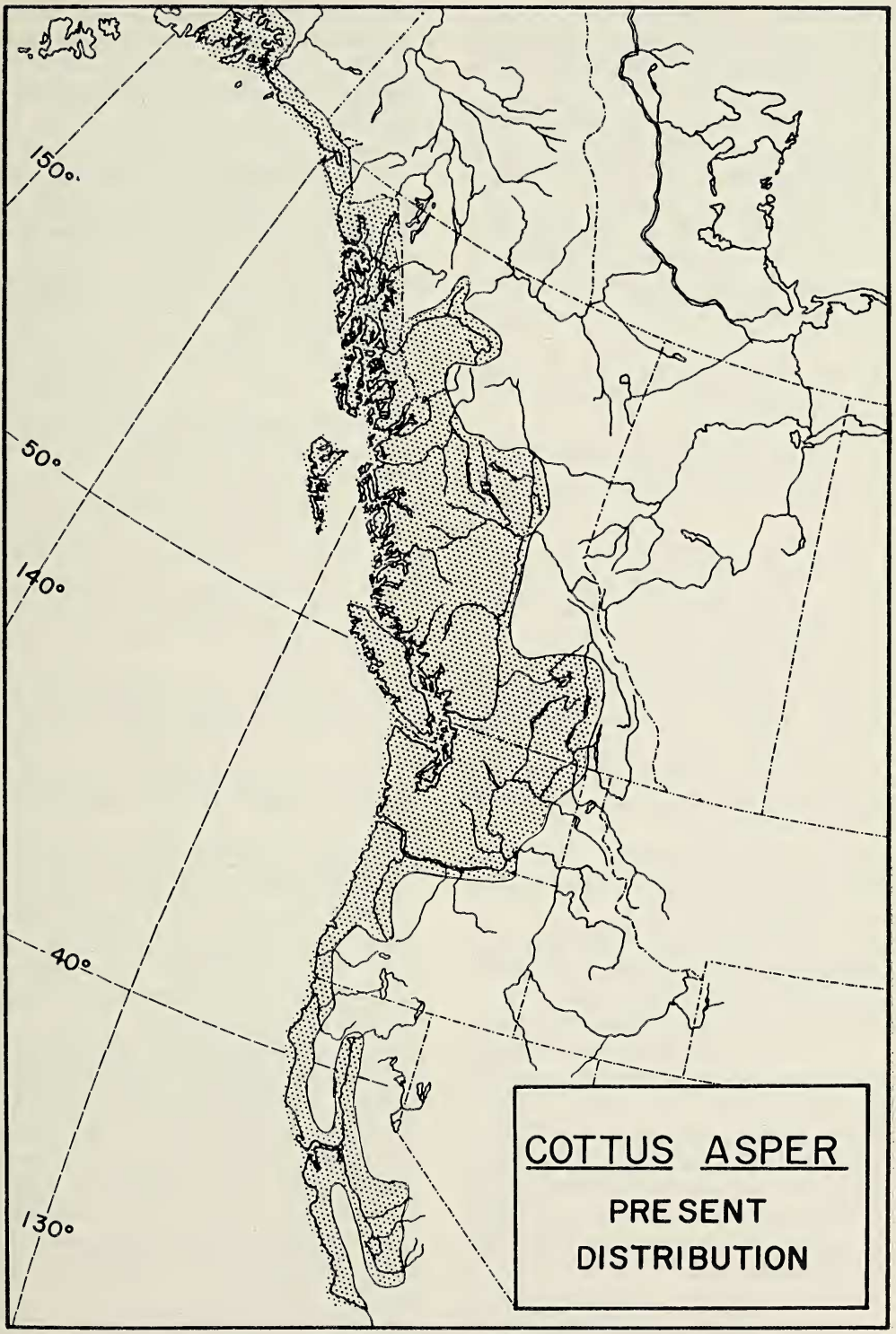

FIG. 1. Distributional range of *Cottus asper*.

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